The mesenterial Filaments of the Alcyonaria.

By

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With Plates 1 and 2.

In studying the development of *Renilla* I was struck by the curious fact that the so-called dorsal pair of mesenterial filaments appear at different periods in the egg-development and in the bud-development.

In the egg-embryo they are the last to appear and develop much more slowly than the other six. In the buds, on the contrary, they are usually the first to appear, and always develop more rapidly than the others.

Since making these observations on *Renilla* — for a description of which I must refer to my paper in the Philosophical Transactions for 1883 — I have made farther observations which lead me to believe that this contrast in development between the egg-embryo and the bud exists in a considerable number of *Alcyonaria*, though not in all. In the egg-embryos of *Leptogorgia virgulata* Edw. and Haime, and *Clavularia ochracea* Koch, the development of these filaments is quite like that of *Renilla*. Hence we have representatives of three leading and widely different groups of *Alcyonaria* — namely, following Koch's classification, the *Cornularida*, *Axifera*, and *Pennatulida* — which agree in this respect; and it appears probable that this mode of egg-development is characteristic of the entire order.

On the other hand, it is certain that in the bud-development the dorsal filaments are the first to appear in many *Alcyonaria* besides *Renilla*; and even where this is not the case, they usually develop more rapidly and always attain a greater length than the other six. For instance, Kölliker observed that these filaments were fully formed in the buds of *Halisceptrum* at a time when not a trace of the other six could be made out, and I have observed the same in the buds of

Kophobelemnon and *Funiculina*. In *Alcyonium* and *Paralcyonium*, the
dorsal filaments make their appearance at about the same time with
the others (see fig. 3). Very soon, however, the dorsal filaments out-
strip the others in development, so that when the bud is not more than
half grown they may be several times as long as the latter (see fig. 4).
In *Gorgonia* the filaments all appear at about the same time, so far as
I could determine, and the dorsal pair become after a time longer than
the others, though much less so than in *Alcyonium*.

In the development of these organs we have therefore a simple but
rather striking case of contrast between the sexual and asexual repro-
duction of an animal, and the structure of the polyps is simple enough
to warrant the hope that it may be possible to discover the c a u s e of
this contrast. For this reason I have studied at Naples the structure
and development of the mesenterial filaments in several genera of *Alcyo-
naria*, and the novelty of the results has been unexpected. The result
of this study has been firstly, as I believe, to show clearly the cause
of the difference between the egg-development and the bud-develop-
ment where this exists: secondly, to demonstrate that among the so-
called mesenterial filaments of the *Alcyonaria* we have to distinguish
two kinds of organs which differ fundamentally in structure, develop-
ment, and function; and thirdly, to suggest certain comparisons between
the *Anthozoa* and the *Enterocoela* which so far as I know have not
hitherto been considered, and which involve an entirely new conception
of the morphology of a polyp.

It has been noticed by nearly all observers of the *Alcyonaria* that
the dorsal pair of filaments are invariably longer and narrower than the
other six. It was observed also that they have a different structure from
the others, though this difference has never been carefully investigated;
indeed the mesenterial filaments in general have been little studied, many
observers contenting themselves with the somewhat vague statement
that »the filaments have the usual structure«. Nevertheless, the dorsal
filaments have always been supposed to be of entodermic origin like
the others — that is, simple thickenings' of the edges of the dorsal
septa, which are purely entodermic structures. I have however found
that while this is strictly true of the six shorter filaments, t h e d o r s a l
p a i r a r e, o n t h e c o n t r a r y, e n t i r e l y o f e c t o d e r m i c o r i g i n,
b e i n g u n m i s t a k a b l y d o w n g r o w t h s f r o m t h e i n v a g i n a t e d
e c t o d e r m o f t h e o e s o p h a g u s. This curious fact, which I suspected
but did not succeed in proving in the case of *Renilla*, shows that the
dorsal filaments are morphologically quite different structures from the

six shorter filaments; and it now appears that their functions are as different as their structure. Before considering the minute structure of the filaments I will briefly describe their arrangement, which so far as known is uniform throughout the group. We may take *Alcyonium* as a type.

Fig. 4 represents from the inner or dorsal side a half-grown bud, in which the dorsal filaments are not yet fully developed, but which will sufficiently well show the arrangement of the organs. The free portion of the polyp — which is still very short — shows through the canals. The eight septa radiate from the oesophagus, *oe*, at nearly equal intervals, bearing upon their edges the mesenterial filaments. Six of these are short and thick, and in older polyps are always thrown into transverse folds. These are the entodermic filaments. The other two, *d.f.*, borne on the dorsal septa, are extremely long, slender and perfectly straight. They extend far back towards the hinder end of the stomach-cavity, one of them being usually longer than the other, as in the figure. These are the ectodermic filaments, or as I shall sometimes prefer to call them, the e c t o d e r m i c b a n d s.

Connecting with the polyp on all sides we see the network of entodermic canals through which it communicates with older polyps on each side, and along the middle dorsal line are the openings of similar canals not represented in the figure. This line of openings corresponds with a partition wall between two mature polyps, over and between which the younger polyp lies, and which for the sake of clearness are not represented in the figure.

The relations of this canal-system to the polyp-cavities vary widely among the *Alcyonaria*, and in these variations lies, as I believe, one of the chief causes of the differences between the bud-development of the various forms.

Methods.

After testing many preservative and staining fluids, the following methods were adopted as giving, upon the whole, the best results. The animals were suddenly killed by momentary immersion in a mixture of one part strong acetic acid and two parts of a concentrated solution of corrosive sublimate in fresh water. After being quickly washed they were transferred to a concentrated solution of sublimate in fresh water and left two or three hours; the internal cavities being injected with the solution, where this was possible. They were then thoroughly washed in running sea-water, then in distilled water, and finally

preserved in successive grades of alcohol. A weak solution of iodine in alcohol and sea-water also gives beautiful results, but is less certain in its action. For staining I have used GRENACHER's alum-carmine, borax-carmine, picro–carmine and KLEINENBERG's haematoxylin. Much the best results are obtained by the use of alum-carmine, but it must be used as quickly as possible, since the gelatinous tissue of the mesoderm is apt to shrink if the object be left too long in aqueous fluids. The tissues were decalcified with very weak nitric or hydrochloric acid in 90 per cent alcohol. For maceration, the HERTWIGS' well-known mixture of osmic and acetic acids gives good results.

I. Structure, development and functions of the six short or entodermic filaments.

a) Structure.

These filaments appear to have essentially the same structure in all of the forms which I have examined, including eleven different genera, and I will select *Paralcyonium* as type. It is not my purpose to give an exhaustive description of their structure, but only to describe their general features.

A transverse section through one of these filaments is shown in fig. 12. The septum, *s*, consists of a delicate lamella, covered on both sides by a pavement-epithelium. In the base of the latter, upon the ventral side, we see muscle-fibres in cross-section. The lamella may be followed out into the filament, where it gradually fades away. The filament is formed by a sudden expansion of the septum, the cells at the same time undergoing a total change of structure. At the back of the filament the cells assume a columnar form, but still remain clear and only slightly granular. At the sides and in front they become elongated and swollen, and their contents undergoes a great change. The cell-bodies stain deeply, so that in most cases the nuclei become obscured. As regards their contents, the cells appear mainly in two forms. In one form the cell is closely packed with deeply stained highly refringent spheroidal bodies. In the other form the cell-contents is only slightly granular and is uniformly and intensely stained. Both forms may be easily and completely isolated by maceration in HERTWIGS' mixture of osmic and acetic acids, and are then seen to bear a single cilium at the outer end, and to contain in the basal part a nucleus like the ordinary entoderm nuclei. At the base they sometimes appear

smoothly rounded, in other cases are attenuated and have short processes which are perhaps continuous with nervous fibrils.

Although typical examples of these two forms of cells are very distinct, there are nevertheless intermediate forms, and I am inclined to regard them as only different conditions in the activity of the same kind of cell. In many cases the cell is sharply contracted in the middle, so as to assume an hour-glass form, the lower division containing the nucleus. In such cells both divisions are sometimes filled with the refringent spheroids, but in other cases the latter are confined to the outer division, and the basal part is clear or slightly granular. Other cells have the usual form but their contents are confusedly granular, showing neither the sharply defined spheroids of the one form nor the uniform structure of the other. In many cases a close examination of the clear cells shows that they also are filled with the spheroidal bodies, but these are so slightly stained as to be barely visible.

These cells are evidently of the same nature as the two forms of »gland-cells« described by the Hertwig brothers in the filaments of the Actinians, with which they agree in all respects except that I have been unable to see the protoplasmic network of the clear cells as plainly as it is figured by these authors.

Scattered irregularly through the filament are minute nettle-capsules (n). They are remarkable for their very small size, being smaller than the nuclei of the entoderm cells. They have an oval form and each contains a spirally coiled filament. In the minuteness and rarity of the nettle-capsules the mesenterial filaments of the *Alcyonaria* differ decidedly from those of the Actinians, and it seems possible that in the former group they are to be regarded as rudimentary organs.

Sensory cells, like those of the Actinians, I have been unable to find. The centre of the filament is occupied by a clear, apparently fibrous mass, in which are considerable numbers of characteristic entoderm nuclei.

b) Development.

I have already described the development of these filaments in *Renilla* (l. c.) — though I failed to perceive their fundamental difference from the dorsal filaments — and obtained strong evidence of their entodermic origin as local thickenings upon the edges of the septa. I found that the rudiments of the filaments, in some cases, made their appearance before the stomodaeum broke through, and while the invaginated ectoderm

was still everywhere separated from the entoderm by the supporting lamella [1]. In later stages however the filaments became perfectly continuous with the inner or ectodermic wall of the oesophagus, and it was owing to this fact that I failed to distinguish between the ectodermic and entodermic filaments, and was led to ascribe an entodermic origin to all of them.

At Naples I have examined the development of these filaments in the buds of *Alcyonium*, *Paralcyonium*, *Clavularia*, *Gorgonia*, *Kophobelemnon*, *Funiculina* and *Pennatula* and have obtained the clearest evidence that they are in all cases of entodermic origin. The best preparations are afforded by *Alcyonium*, which I will therefore first describe. In fig. 10 we have a longitudinal section through a bud of *Alcyonium*, showing the first rudiment of one of the ventral filaments at *e.f.* The same filament is represented more highly magnified in fig. 11. The ventral wall of the stomodaeum is shown in longitudinal section at *v.w.* It is composed of closely set, very long, columnar, ciliated ectoderm cells, each with a small oval intensely staining nucleus. Following these cells towards the inner opening of the oesophagus, we find that at the beginning of the septum they bend over the lower lip of the oesophagus and become continuous with the edge of the septum. The cells retain their characteristic peculiarities as far as the lip, but at this point undergo a decided change. In the region marked *in.* the cell-outlines cannot be distinguished, the nuclei become pale and indistinct and finally disappear. Then the characteristic entoderm nuclei suddenly appear, which differ entirely from those of the stomodaeal ectoderm. They are nearly twice as large as the latter, are only slightly oval, and stain very feebly. The outlines of the cells can only here and there be distinguished. They are polygonal or fusiform, and as shown in transverse sections, form a thin pavement epithelium. Altogether, the contrast between the cells of the septum and of the stomodaeum is unmistakeable.

Following the septum downwards we pass over a considerable region in which the edge of the septum is not at all thickened and is covered by ordinary entoderm cells. Just above *v* we find a few of the elongated characteristic »gland cells«, and a little farther down, at *e.f.*, is a considerable accumulation of these cells, forming the first rudiment of the filament.

These facts render it nearly certain that the filament is simply a

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[1] See Phil. Trans. 1883, Pl. VIII, fig. 137, and Pl. XI, fig. 159.

local thickening of the edge of the septum. It seems incredible that
the region between the stomodaeal ectoderm and the filament consists
of ectoderm cells, derived from the former, which have lost their own
characteristics and completely assumed those of entoderm cells, and
this hypothesis is disproved by the following observations on *Funiculina*.
In fig. 13 the entodermic filaments have not yet appeared in the
youngest bud, A. As in *Alcyonium* we can follow the stomodaeal ecto-
derm, *v.w.* down to the lip of the oesophagus, where it becomes
continuous with the border of the ventral septum, *v.s.* The contrast
between the stomodaeal and the septal cells is of the same nature as in
Alcyonium, though rather less marked. Beyond the lip we find only
entoderm cells, and the limit between the two kinds of cells is some-
times sharply defined. In the next older bud, B, we observe quite simi-
lar facts, but the edge of the ventral septum is slightly thickened at *e.f.*
some distance down the septum, and the nuclei are somewhat crowd-
ed. Finally, in the oldest bud, C, this thickening is more pronounced,
and is shown to be the filament by the fact that it already contains so-
lid food-particles inclosed in vacuoles, *v.* (see the following account of
the functions of these filaments). There is no evidence whatever of a
downgrowth of ectoderm cells, but the filament arises quite indepen-
dently of the stomodaeum.

In *Kophobelemnon*, fig. 5, we find similar facts. In this case the
entodermic and ectodermic nuclei are nearly of the same size but the
contrast between the stomodaeal and septal cells is rendered very dis-
tinct by the circumstance that the latter contain considerable quantities
of a yellowish pigment, in the form of small highly refringent pigment
granules, which is completely absent from the former. The rudiment
of the filament is shown at *e.f.*, at some distance from the oesophagus,
and it consists entirely of entoderm cells. Below it, at *ov.*, are two em-
bryonic ova.

These observations, taken in connection with those on *Renilla*,
render it certain, I think, that the six short filaments have no-
thing to do with the stomodaeum and are strictly ento-
dermic structures. The region marked *in.* in fig. 11 marks the
limit between the ectoderm and entoderm cells, and apparently consists
of partially or completely degenerated cells, originally derived from
the stomodaeum.

c) Function.

Passing over the fantastic views of many early writers, we find

it to be now generally recognised that the mesenterial filaments of polyps in general play an important part in the functions of digestion — though exactly how, and to what extent, has until very recently been a matter of pure conjecture, owing to the great difficulty of observations upon living animals, and the lack of precise anatomical knowledge. The brothers HERTWIG, after studying in the most masterly manner the structure of many Actinians, came to the conclusion that the mesenterial filaments of these animals are at least very important organs of digestion; but exactly how their functions are performed was not determined, since their studies were anatomical rather than physiological. Much the most important evidence upon the subject has been brought forward by KRUKENBERG [1]. His important conclusion, based upon the physiological study of a considerable number of Actinians, is that t h e m e s e n t e r i a l f i l a m e n t s a r e n o t o n l y u n q u e s t i o n a b l y org a n s o f d i g e s t i o n , b u t t h e y a r e t h e o n l y o r g a n s o f d i g e s t i o n .   His extensive experiments appear nearly or quite conclusive upon this all-important point. He found, farthermore, that digestion takes place only when the food comes into actual contact with the filaments, and that during digestion the filaments are wound about the food (»u m s t r i c k e n«).

So far as I am aware, I was the first directly to observe the action of the filaments during digestion, in the case of the Gorgonian *Leptogorgia virgulata* Edw. and Haime [2]. A young transparent polyp was fed with oyster eggs and observed under the microscope. The food was held for two or three hours closely clasped by the mesenterial filaments w h i c h w e r e d r a w n c l o s e l y t o g e t h e r a r o u n d t h e m a s s o f e g g s in the upper part of the stomach. Afterwards, a mass of refuse matter was passed out through the oesophagus and the filaments resumed their ordinary position. In this young polyp the dorsal filaments were still rudimentary. So far as could be determined t h e e n t o d e r m o f t h e r a d i a l c h a m b e r s t o o k n o p a r t i n t h e p r o c e s s o f d i g e s t i o n , w h i c h w a s e n t i r e l y p e r f o r m e d b y t h e s i x e n t o d e r m i c f i l a m e n t s .   This is entirely in accord with KRUKENBERG'S studies upon the Actinians.

Since these observations upon *Leptogorgia* (which have been long delayed in press) A. MILNES MARSHALL and WILLIAM P. MARSHALL

[1] Vergleichend-Physiologische Studien an den Küsten der Adria, I. Abtheilung, Heidelberg, 1880.

[2] Phil. Trans. 1883, p. 64.

have discovered, in *Pennatula* and *Virgularia*, foreign bodies, such as diatoms, actually embedded in the filaments[1]. Although they do not state in which filaments these bodies were found, it is clear from their figures that it was in the entodermic filaments. This indicated that during digestion solid matters are taken bodily into the filaments, and are probably actually engulphed by the cells *Amoeba*-fashion, as in many other *Coelenterata*. This very important observation I can fully confirm in *Alcyonium*, *Paralcyonium* and *Funiculina*, where diatoms and other solid foreign bodies may with the greatest clearness be seen enclosed in vacuoles within the entodermic filaments. In fig. 12 (*Paralcyonium*) we see a diatom and three other foreign bodies entirely imbedded in the substance of the filament, and similar bodies are seen at *v* in fig. 11 and 13. It is impossible to determine whether these bodies lie within or only between the cells, but the former seems from analogy probable. In *Paralcyonium* these bodies are sometimes very abundant, but they are always confined, so far as I have observed, to the entodermic filaments and never are found either in the dorsal filaments or in the general entoderm covering the septa and the body-wall.

From these facts it seems very probable that the digestive functions are performed by the entodermic filaments alone and never by the ectodermic filaments or the general entoderm. This conclusion accords entirely with the histological structure of these organs, and so far as the ectodermic filaments are concerned, is what we might expect from their embryological origin. The large granular cells, usually described as glandular, which form the great mass of the entodermic filaments, I am inclined to regard as cells which act like so many *Amoebae*, taking solid particles into their interior and there digesting them. In the ectodermic filaments such cells do not exist; and although it is difficult to prove a negative in such matters, the structure of the ciliated cells of which they are composed (see part II) is such as to indicate anything rather than a digestive function. The same is true of the general entoderm covering the septa and the body-walls. As I have said this entoderm has usually the form of a pavement-epithelium (compare figs. 5, 10, 11, 12). In some genera this epithelium is exceedingly thin, as in *Alcyonium* and *Paralcyonium*. In others it is thicker, either everywhere or in parts, especially in the upper part of the body-wall, and in some forms it be-

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[1] Report on the Oban *Pennatulida*, Birmingham, 1882.

comes even columnar, though never to the same extent as in the Acti-
nians. I am inclined to believe that this depends to some extent upon
the state of contraction, and that when the polyps are fully expanded
the epithelium is always comparatively thin. So far as I have seen, no
gland-cells like those of the entodermic filaments are found in this
epithelium, and no evidence of intra-cellular digestion can be discov-
ered. Most of the cells composing the epithelium produce muscle-
fibres at their inner ends — that is, they are myoblasts — and I have
brought forward evidence (Development of *Renilla*, l. c.) to show that
nearly or all of the musculature of the *Alcyonaria* is entodermic.

This histological differentiation in the entoderm I believe to be a
fact of great significance, as pointed out in part V.

II. Development, structure and function of the dorsal or ectodermic filaments.

a) Development.

I have already shown that in *Renilla* and *Leptogorgia* the dorsal
filaments first appear as two slight prominences upon the dorsal lip
of the oesophagus [1], whence they grow backwards along the edges of
the dorsal septa until they reach the posterior end of the polyp (or in
Renilla the posterior end of the so-called polyp-cell). The same is
true of *Clavularia*, as shown in fig. 1. The dorsal filaments, one of
which is shown at *d.f.*, appear as two short prolongations from the lips
of the oesophagus, and in later stages gradually extend downwards to
the bottom of the stomach-cavity, but without losing their connection
with the oesophagus. If a longitudinal section be made through the
oesophagus and these rudimentary filaments, the latter are found to be
simple continuations of the inner or ectodermic layer of the former.
Their cells agree exactly with those of the inner layer of the oesophagus,
and there is not the slightest trace of a limit between them; it is in
fact impossible to say where the filament begins. On the other hand,
they differ totally from the entoderm cells of the septum. The latter
are flat and polygonal with large pale nearly round nuclei. The cells
of the filament and of the inner layer of the oesophagus are of a high
columnar form and possess small oval nuclei which stain very intensely.
The contrast between these two kinds of cells is most striking and
in properly prese.ved specimens appears at the first glance.

[1] Phil. Trans. 1883, figs. 117, 177.

The cells of the filament retain their characters in later stages, are uniform from one end to the other, and always may be followed directly up into the inner wall of the oesophagus. Hence there can be no doubt that the dorsal filaments of the egg-embryo are morphologically nothing but narrow prolongations, along the septa, of the inner layer of the oesophagus; and the latter is agreed by all observers to consist of ectoderm invaginated from the exterior.

Turning now to the development of the buds, we find precisely similar facts. In a very young bud of *Funiculina*, for instance (fig. 13, A) the dorsal filaments, *d.f.*, appear as slight knob-like outgrowths from the inner layer of the oesophagus. Everything I have said of the young dorsal filaments of *Clavularia* will apply equally well to the present case, and need not be repeated. A later stage in the bud of *Alcyonium* is shown in fig. 10. The dorsal filaments, *d.f.*, are considerably longer, and the six other filaments, one of which is shown at *e.f.*, have appeared. The histological structure is the same as in *Clavularia* in every detail, except that the contrast between the ectodermic cells of the filament and the entodermic cells of the septum is even more striking.

A still later stage in the bud of *Funiculina* is shown at B., fig. 13. The ectodermic filaments, *d.f.*, now extend to the bottom of the stomach-cavity, but their structure is quite unaltered and the characteristic columnar cells may be traced up without a break into the inner layer of the oesophagus, so that it is not possible to say where the filament begins. An older bud is shown at C, fig. 13, and a still later stage of *Kophobelemnon* in fig. 5. In the latter, especially, the dorsal filaments have attained an enormous length, but the histological characters are unchanged. In sections stained with GRENACHER's alum-carmine or with haematoxylin, the contrast in appearance between these filaments and the entodermic structures is most striking. The former appear of an intense blue or purple color, from their closely-crowded deeply-stained nuclei, whereas the entodermic structures are pale, granular, usually much pigmented, and contain a much smaller number of nuclei. These facts show beyond the possibility of doubt that in the buds, as in the primary polyp, the dorsal filaments are ectodermic structures and are morphologically downgrowths from the stomodaeum.

If we examine the rudimentary individuals or zooids of the *Pennatulida* we find quite similar facts. It is a well known discovery of KÖLLIKER that the zooids of many species possess a single pair of fila-

ments, and KÖLLIKER has shown that these filaments correspond with
the dorsal pair of the sexual polyps. I have examined the structure of
these filaments in the zooids of *Pennatula*, *Funiculina* and *Kophobelem-
non*, and find that they agree entirely in structure with those of the
sexual polyps. Like the latter, t h e f i l a m e n t s o f t h e z o o i d s a r e
d o w n g r o w t h s f r o m t h e s t o m o d a e u m a n d a r e t h e r e f o r e
e c t o d e r m i c s t r u c t u r e s. Their cells are of a high columnar form
with small intensely staining nuclei, and in longitudinal sections they
are found to be continuous with the dorsal ectoderm of the stomodaeum.
In fact, a longitudinal section through a zooid is absolutely indistinguish-
able from a corresponding section through a young sexual polyp before
the appearance of the entodermic filaments, and A and B, fig. 13, would
do equally well for figures of zooids, except for the rudiment of an
entodermic filament in B.

b) Structure.

A comparison of the ectodermic filaments in various genera of
Alcyonaria shows that they have almost precisely the same structure
throughout the group. To illustrate this similarity I have given figures,
drawn to the same scale with fig. 12, of transverse sections of these
filaments in the sexual polyps of *Gorgonia* (fig. 6), *Paralcyonium* (fig. 8),
a zooid of *Kophobelemnon* (fig. 9), and a young polyp of *Funiculina*
(fig. 7). A glance at these figures shows that the structure is essentially
the same in all — though these genera represent three widely different
families — and differs entirely from that of the entodermic filaments
(fig. 12). The filament consists of two entirely different portions.
Much the greater part consists of high columnar cells, each with a small
oval intensely stained nucleus and a single powerful cilium at the outer
end. The nucleus is usually situated in the middle or basal part of the
cell and seldom in the outer third; so that in sections the outer part of
the filament appears clear, contrasting sharply with the inner two thirds
where the nuclei are closely packed together. These cells are quite
similar to those of the inner layer of the oesophagus, and obviously
represent the ectodermic downgrowth from the stomodaeum.

The columnar cells are arranged so as to form a long solid band
on the edge of the septum, which I shall call the e c t o d e r m i c b a n d.
As seen in sections, this band has a bilobed form — or in other words,
a longitudinal groove runs along its middle. The form of the groove
varies greatly according to the state of contraction. The most usual
form is shown in fig. 7 (*Funiculina*), but the groove may be much more

pronounced, so that the band assumes a Y-form, or it may be completely obliterated, as in fig. 8 *(Paralcyonium)*. It is difficult to determine its exact form in living specimens, but it is certain that the groove is usually very distinct.

The nuclei of the band are arranged in two lateral groups to correspond with the two external lobes. Between these two groups is a clearer obscurely triangular mass, the structure of which I have not been able clearly to make out, but which would well repay investigation. In *Gorgonia* a few pale rounded bodies may be seen in it, which are apparently nuclei. In *Paralcyonium* very similar nuclei occur, and in addition a number of bodies which have the appearance of columnar cells. It is possible that these structures may be some kind of a nervous apparatus.

The second part of the filament consist of ordinary flattened epithelial cells like those covering the faces of the septa. As the supporting lamella reaches the ectodermic band the entoderm cells spread out on each side in a thin layer covering the back of the band. They spread out laterally for some distance and then end abruptly. Usually they form only a single layer, but in *Gorgonia* (fig. 6) the cells are in some places more than one layer deep. They differ in no respect from the ordinary entoderm cells, and usually have a flattened form.

The contrast between the entodermic and ectodermic elements of the filament is very striking and is so clearly shown in the figures that no description is necessary. In *Gorgonia* especially (fig. 6) the two kinds of cells are extremely unlike; in other genera the difference is not so great, but is nevertheless apparent at a glance. Of the very marked difference between the cells in their behavior towards staining fluids I have already spoken.

c) Function.

The embryological origin of the ectodermic filaments, the absence of »gland-cells« and of foreign bodies, and the fact that these filaments alone appear in the zooids of *Pennatulida* (which so far as known take no part in the ingestion of food) form a rather strong body of evidence that they are not concerned in the process of digestion. Their structure at once suggests that they are organs of circulation, and direct observation, so far as it goes, confirms this suggestion.

If a fully expanded living polyp of *Alcyonium* or *Paralcyonium* be examined under the microscope, the currents in the gastric fluid can easily be observed. The general direction of these currents is upwards

along the septa and body-wall, and downwards in the middle of the stomach-cavity and along the entodermic wall of the oesophagus. If the entodermic filaments be closely examined, they are not found to produce strong and definite currents, though they are sparsely ciliated. Indeed, this would be nearly impossible because they are constantly changing their form as they are thrown into various convolutions by the contractions of the septa. The straight ectodermic filaments present a very different appearance. Along the ectodermic bands we may observe constant and powerful upward currents, which may be clearly seen by observing the particles suspended in the gastric fluid. These particles often get into the groove of the filament and may be followed, sometimes for a long distance, as they move rapidly up- wards. In one case I observed a *Paralcyonium* in which the gastric fluid was so heavily laden with particles as to appear quite cloudy. In the grooves of the ectodermic bands constant processions of these parti- cles could be seen coursing rapidly upwards and following the slight undulations of the filaments with the greatest precision. At the upper extremity the currents are discharged upon or into the lower end of the oesophagus, which is usually held widely open, and then join the de- scending currents along the middle of the gastric cavity.

I was so fortunate as to procure a small transparent specimen of *Veretillum* in which the circulation could be clearly seen. In the sexual polyps the circulation was precisely as in *Alcyonium*. The zooids, as in many other *Pennatulida*, possess a well-developed pair of dorsal filaments. The currents along the ectodermic bands in the zooids, as in the sexual polyps, are directed strongly upwards.

These observations are enough to afford a strong presumption that the action of the cilia of the ectodermic bands is upwards in a large number of *Alcyonaria*, since it is true in the *Alcyonida* and *Pennatulida* and in the zooids as well as in the sexual polyps, and the dorsal filaments have everywhere the same structure and relations. Moreover, it follows that the same is probably true in the young buds, which, as I have elsewhere pointed out, are identical structurally and physiologically with the zooids of *Pennatulida*.

Whether the direction of the currents is ever reversed I do not know, but I have examined many different individuals at different times and have always found it constant. This may possibly happen when the polyps are contracted, but in this condition they cannot be observed.

The general entoderm is also ciliated, but to what extent I cannot

say, since the cilia, unlike those of the dorsal filaments and of the sto-
modaeum, cannot be well preserved and are not visible in sections. I
think it probable from a study of living animals that the general currents
of the gastric fluid are produced by the cilia of the general entoderm,
and tend simply to keep this fluid everywhere uniform. The object of
the currents produced by the ectodermic bands is probably more special,
as pointed out in part III.

III. Application of these results to special morphological problems.

We are now in a position to consider the question why the dorsal
filaments should show a tendency to earlier and more rapid development
in the buds, and we have not far to seek for the answer. The egg-
embryology may be taken to represent more nearly the phylogenetic
development, and the presumption is that the late appearance of the
dorsal filaments is the more primitive condition — a conclusion support-
ed by other considerations given in part IV. Hence their early devel-
opment in the bud is probably due to some special physiological condi-
tion existing in the bud and not in the egg-embryo. A moment's con-
sideration shows that this condition is the need for food. All known
egg-embryos of *Alcyonaria* are abundantly supplied with deutoplasm
which is sufficient for their needs until the young polyps are able to
eat for themselves. The bud-embryo, on the contrary, has
no deutoplasm but is dependent upon nutritive fluids
brought from the feeding-polyps by the circulatory organs.
Hence the early development of the ectodermic filaments,
and hence also their appearance in the zooids of *Penna-
tulida*, which remain permanently in the condition of
young buds. The zooids progress in their development simply to
the point where their circulatory organs become established. To ad-
vance beyond this point would be a sheer waste, since the entodermic
or digestive filaments would be of no use to an organism which never
takes in food from the exterior.

We can now understand why the action of the cilia of the ectoder-
mic bands should always be upwards. It has been pointed out especi-
ally by Koch[1] that the budding of the *Alcyonaria* is seldom or never

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[1] Anatomie der *Clavularia prolifera*, nebst einigen vergleichenden Bemerkun-
gen, Morph. Jahrb. Bd. IV, p. 467.

direct. That is, the buds do not as a rule arise as direct outgrowths
from older polyps, but by means of an interposed network of entoder-
mic canals. This is shown for instance in fig. 3, where the young polyp
is seen to arise in the middle of a canal-system which communicates
with the cavities of older polyps.

Now we find, as a rule, that the canal-system communicates with
the b a s a l p a r t of the zooid or young bud (see fig. 13), and hence the
food-supply must enter at this part of the bud. The most active part of
the bud or zooid is however at the opposite end where the powerful
ciliated cells of the oesophagus, which draw in the water, are in a state
of intense though intermittent activity, and where the organs of the
young polyp are developing. It seems therefore clear that it must be
advantageous to have strong and steady currents flowing from the basal
to the upper part of the stomach-cavity — and this is effected by the
ectodermic bands of the dorsal filaments. In some cases these organs
actually extend out into the canal system. In fig. 5 (*Kophobelemnon*)
the enormously developed dorsal filaments, *d.f.*, extend far out into
the canal-system. The communications of this system with the main longi-
tudinal canals of the colony are shown at *a, a, a*, and an inspection of
the figure will show, I think, that the upward currents along the ectodermic
bands must tend to transport the nutritive fluids from the canal system to
the upper portion of the bud where development is actively going forward.
In other cases the dorsal filaments may be followed down to the very
mouths of the canals, but there stop, as I have observed in *Gorgonia*.

As a rule, however, the dorsal filaments extend only to the base of
the polyp, as shown in fig. 13, but even here it seems clear that their
action must tend to bring about the same result. In the adult polyps
this is always the case, so far as known, and we can now understand
the object of this arrangement. It must often happen that certain polyps
of a colony obtain a larger supply of food than others, though it is
clearly advantageous that all should be equally well-fed. The nutritive
fluids derived from these polyps must pass into the canal-system, though
we are entirely in ignorance as to how this is effected — whether by
the contraction of the polyps, or by a reversed action of the cilia, or by
a specialisation of certain canals for this purpose. But, however this
is effected, it seems pretty clear that the less well-fed polyps profit by
the fact that the ciliated bands extend down to the region where they
communicate with the canal-system.

We may now inquire after the cause of the exceptions to the gene-
ral rule that the dorsal filaments are the first to appear in the buds, and

why it is that the zooids of some *Pennatulida* do not possess these organs. The defective state of our anatomical knowledge will not admit of a complete explanation, but in most cases it appears tolerably clear. In *Alcyonium* the cause appears to lie in the circumstance that the canal-system communicates on all sides with the bud, which moreover lies at the same level with the canals. We see in fig. 3 that the dorsal filaments, *d.f.*, are still rudimentary, though the entodermic filaments are well-developed. If we compare this figure with fig. 13 (*Funiculina*) we see that the relation of the bud to the canal-system is entirely different in the two cases; so that, while in *Funiculina* the upward currents are clearly advantageous, in *Alcyonium* they could be of no use. Hence the rudimentary state of the dorsal filaments in the latter. If, now, we examine a later stage of *Alcyonium* (fig. 4) we find that the dorsal filaments, *d.f.*, have far outstripped the others. We find also that the bud has now a different relation to the canal-system. The canals still communicate on every side with the bud, but the latter has elongated in such a way that the oesophagus and growing parts are situated quite at the upper end. The principal nutritive supply must hence come from below, and the dorsal filaments have therefore elongated to produce the necessary upward currents.

If the position of the dorsal filaments be examined it is found to be the most advantageous possible. The canal-system communicates with the polyp not only along the sides but also along the middle dorsal line through the round openings represented in the figure between the dorsal filaments. Hence each filament lies between two rows of openings, and the advantage of this arrangement is obvious.

We may now consider two other exceptions namely *Paralcyonium* and *Gorgonia*. Here, as in *Alcyonium*, the dorsal filaments appear at the same time with the others, and only in later stages become distinctly longer. The case seems a difficult one at first, because here as in *Funiculina*, the communication with the canal-system is at the base of the bud. But the explanation is clear, though different from that of the *Alcyonium*-development. The canal-system of *Paralcyonium*, as pointed out by KOCH, is reduced to a to nothing more than a series of large holes which open directly into the cavity of the older polyp. The currents of the latter can therefore flow directly into the bud, as I have observed in living specimens. In fact, the bud is only separated from the main polyp by two or three delicate strands of tissue which can scarcely afford a resistance to the passage of the nutritive fluids. More-

over, the oesophagus extends far downwards, so that the dorsal fila-
ments, even when very short, extend nearly to the base of the bud.
Hence the upward currents are unnecessary until the bud elongates con-
siderably, and the ectodermic bands therefore elongate only in later
stages.

In *Gorgonia* the canal-system is well-developed, but the oesopha-
gus extends even farther inwards than in *Paralcyonium*. Hence in this
case also the upward currents are at first unnecessary and the elon-
gation of the filaments takes place only in later stages.

Turning now to the zooids of the *Pennatulida* we find similar
conditions. The general rule is that they communicate by their
bases with the canal-system, and the dorsal filaments, when present,
extend to the bottom of the stomach-cavity, sometimes attaining an
enormous development. If my hypothesis be correct, we should expect
to find in those zooids which do not possess the filaments, special phy-
siological conditions which obviate the need for definite upward cur-
rents. I have myself investigated only one such case — the zooids
namely of *Renilla* — and we can here clearly perceive such conditions.
The zooids of *Renilla* are not elongated and open directly
into the cavities of the feeding polyps without the inter-
position of a canal-system[1], so that as in the young bud of *Par-
alcyonium* the fluids can pass directly into the zooid.

For the zooids of other *Pennatulida* I must refer to KÖLLIKER's
great work, in which however the anatomical relations are not always
described with sufficient minuteness to clear up the present point.
Looking through his descriptions we find that the zooids can be thus
grouped:

A. Zooids with filaments.

Pteroides (zooids of the »Zooidplatte«)

Pennatula	*Funiculina*
Ptilosarcus	*Kophobelemnon*
Halisceptrum	*Policella*
Pavonaria	*Veretillum*
Halipteris	*Stylobelemnon*

B. Zooids without filaments.

Pteroides (Ventral zooids, zooids of the »Kiel« and of the upper face of
the leaves).

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[1] See also KÖLLIKER's Pennatuliden, p. 273.

| *Leioptilum* | *Virgularia* |
| *Sarcophyllum* | *Acanthoptilum* |

Renilla

With the single partial exception of *Stylobelemnon*, in which some of the zooids are said to open directly into the sexual polyps, the zooids of list A communicate at their bases with the feeding polyps only through the finer canal-system.

We will examine separately the zooids of list B.

The case of *Pteroides* is very important since both forms of zooids coexist in the same colony. Those of the »Zooidplatte«, which alone possess filaments, open into a spongy network of canals. All of the other zooids open either directly into the feeding polyps, or by means of a short canal, directly into the main longitudinal canals. This is obviously a strong confirmation of my hypothesis. The zooids of *Virgularia* are stated to open either directly into the polyps, or in some cases into the canal-system. The anatomical relations of *Acanthoptilum* are not described, and the case of *Renilla* I have already considered. The zooids of *Leioptilum* and *Sarcophyllum* possess no filaments and nevertheless open into the canal-system. This case I am unable to explain as it stands.

Upon the whole, I think, these facts lend support to my hypothesis, as to the office of the filaments in the zooids; and the case of *Pteroides* tells strongly in its favor. It may perhaps be justifiable to expect that the two adverse cases may in future be explained by the discovery of special conditions which cannot be perceived from KÖLLIKER's brief and general descriptions.

Lastly we may consider the significance of the position of the ciliated bands. It is a striking fact that in *Alcyonarian* colonies the dorsal radial chamber appears to be always turned in a definite direction. In the penniform *Pennatulida* it seems to be always turned forwards — i. e. towards the tip of the colony. In compact colonies, like *Sarcophyton*, *Heliopora*[1], *Alcyonium*, *Paralcyonium*, the dorsal chamber is turned towards the axis of the colony in the »polyp-cell« and hence upwards in the free part of the polyp. The same is true of *Veretillum* which forms a compact mass like an *Alcyonium* branch. The foregoing considerations enable us to understand why the ectodermic bands should be placed upon the dorsal septa. If we examine a branch of *Alcyonium* (fig. 15) we observe that the young buds, *p.*, always arise in the angle between two older buds

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[1] MOSELEY, Phil. Trans. Vol. 166, Part I, p. 121.

— that is directly over the partition which separates the latter — and in cross-sections we find that the young buds overlap, to some extent, the older buds, so as partially to include them within the branch. If we follow out in imagination the farther growth of the colony, we see that sooner or later the older polyps must become enclosed within the branch by the younger ones lying outside them. Hence each polyp is at the sides and within the branch (i. e. the side turned towards the axis) adjacent to two older polyps. The canal-system, by which the younger and the older polyps communicate, lies partly at each side of the former, and partly in the partition between the two older polyps, opening into the young polyp along the sides and along the middle dorsal line as shown in fig. 4. A little consideration will show that if the office of the ectodermic bands be to conduct the nutritive fluids derived from older polyps to the upper part of the young bud, then their most advantageous position is on the dorsal septa, since in the typical arrangement, as shown in fig. 4, each dorsal septum lies between two rows of openings by which the nutritive fluids make their entrance. This explanation will apply also to other compact colonies.

If, as seems probable, a form like *Veretillum* has given rise to the penniform *Pennatulida* through forms resembling *Kophobelemnon*, then the position of these filaments in the Penniformes is probably due to simple inheritance. We can perhaps explain the fact that in some of the Penniformes the dorsal filaments are extremely unequal. In fig. 14 I have diagrammatically represented six polyps from a leaf of *Halisceptrum*, as described by KÖLLIKER. Each polyp has one long and one short filament. The six polyps fall obviously into two groups of three, in each of which the oldest is at the right. In some cases these groups consist of as many as seven or eight polyps. The polyp-cavities open directly into one another by perforations in the partition-walls between them, as represented by the broken lines in the diagram.

The important point to observe is that in each polyp the filaments on the right side extend along the whole length of the partition which separates it from an older polyp; and the advantage of this arrangement is obvious when we consider the direction of the currents. This arrangement is probably to be regarded as a secondary one specially acquired by some of the Penniformes.

IV. Phylogeny of the mesenterial filaments.

The late appearance of the dorsal filaments in the egg-embryology

indicates that they have been acquired at a recent period, and later than the entodermic filaments. From the nature of their function it is highly probable that they only assumed their present structure after the establishment of the colony-forming habit, and we can therefore hardly expect to find exactly similar organs in the Actinians. Through the courtesy of Dr. ANDRES I have been enabled to examine sections of *Edwardsia*, an eight-rayed solitary polyp which is in certain respects intermediate in structure between the Actinians and *Alcyonaria*. So far as could be observed the eight filaments are quite similar, and the same is true of the more typical Actinians. We should expect to find the same in solitary *Alcyonaria* like *Monoxenia*, provided these are primitive forms. It is however quite possible that the solitary *Alcyonaria* have lost the habit of forming colonies, and in this case we should expect to find the usual arrangement as a result of inheritance. On the other hand, it would be most interesting to search for the analogues of the ectodermic bands among the colony-forming *Zoantharia*.

The HERTWIG brothers have described the filaments of Actinians as consisting of three portions (as seen in transverse section). The middle part (»Nesseldrüsenstreifen«) consists largely of »gland-cells« and nettle-cells, is closely similar in general structure to the entodermic filaments of *Alcyonaria*, and is believed by the HERTWIGS to be especially concerned in the process of digestion. The two lateral lobes (»Flimmerstreifen«), on the other hand, possess to the minutest detail the histological structure of the ectodermic bands of *Alcyonaria*, and are believed to be organs of circulation.

I would suggest that it is in a high degree probable that the lateral lobes or »Flimmerstreifen« of Actinians, at least in the principal or complete septa, are the homologues of the ectodermic bands of *Alcyonaria*, and are likewise ectodermic downgrowths from the stomodaeum, and that the central lobes or »Nesseldrüsenstreifen« are homologous with the entodermic filaments. As the HERTWIGS have described[1], if we follow the filament upwards towards the oesophagus the central lobe disappears and only the lateral lobes remain. The filament is then closely similar to the dorsal filaments of *Alcyonaria*, which are always bilobed. If we follow the filament downwards, the lateral lobes disappear and the middle lobe remains.

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[1] Jenaische Zeitschr. XIV, 1880, p. 561.

The filament is then essentially similar to the entodermic filaments of *Alcyonaria*.

The truth of this surmise can only be tested by embryological studies, and it is a source of the greatest regret to me that Dr. ANDRES's very important studies upon the embryology of Actinians are still too incomplete to be decisive upon this point. I have however his permission to state that he has a c e r t a i n a m o u n t o f 'e v i d e n c e t h a t t h e u p p e r p a r t o f t h e f i l a m e n t s o f t h e s i x p r i n c i p a l s e p t a i s d e r i v e d b y a d o w n g r o w t h f r o m t h e e c t o d e r m o f t h e s t o m o- d a e u m. If this is shown to be true by later studies it will practically establish the homology here proposed and will be a most important indication of the descent of *Alcyonaria*.

HEIDER [1] came to the interesting and important conclusion that the filaments of *Cerianthus* are entirely of ectodermic origin, on the ground that they are continuous with the inner layer of the oesophagus and possess the same histological structure. But the HERTWIGS justly object that this conclusion cannot be accepted on histological grounds alone and without knowledge of the embryology, and it is farthermore partly in direct opposition to their observation that the filaments of *Cerianthus* possess the usual three portions. The HERTWIGS object farther that in *Sagartia parasitica* the filaments have the same structure upon the incomplete septa which do not reach the oesophagus, so that an ectodermic origin in this case would seem to be excluded. This may be true of the incomplete septa, but I cannot agree with the HERTWIGS that it is therefore necessarily true also of the complete septa.

If my comparison be a just one, then the phylogenetic origin of the ectodermic filaments of *Alcyonaria* may readily be explained. There can be no doubt that the compound *Alcyonaria* are derived from solitary forms, which probably possessed eight similar filaments, each consisting of an ectodermic circulatory part and an entodermic digestive part. As the colony-forming habit became established, bringing with it the need for specialised organs of circulation, a physiological division of labor took place among the filaments. In the dorsal pair the ectodermic part gradually supplanted the entodermic, while the reverse process took place in the other six. We might naturally expect to find some record of this in the embryology, but the investigation has great inherent difficulties and I have not been able to find such a record. Possibly the

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[1] *Cerianthus membranaceus* Haime, Ein Beitrag zur Anatomie der Actinien. Sitz. der k. Akad. d. Wiss., I. Abth. März-Heft, Jahrg. 1879.

region of degenerated ectoderm cells marked *in.* in fig. 11, represents the original ectodermic part of the ventral filament, but this is uncertain.

V. The relations of the Anthozoa to the Enterocoela.

The fact that the digestive functions are confined to the mesenterial filaments suggests certain comparisons between the *Anthozoa* and the higher animals to which I wish to call attention, not by way of setting up a completely formulated theory, but only as a suggestion for farther investigation of the facts.

If we consider the entodermic filaments or their representatives physiologically, we must regard them as the representatives of the alimentary canal of higher animals, and I would suggest that they are not only physiologically but also morphologically the equivalents of the enteron of Enterocoela. If we imagine the filaments to fuse together by their edges and lower extremities, we should have a digestive tube, surrounded by closed cavities in the walls of which are developed the muscles. During digestion, as I showed in the case of *Leptogorgia*, the filaments are closely approximated around the mass of food, so that when in this condition they practically form a tube. And I have observed in two different genera that the filaments do sometimes actually fuse together, as shown for instance in *Alcyonium*, fig. 3, at *v.l.f.*

If this be so, then the radial chambers of an Anthozoan correspond with the mesodermic diverticula of *Enterocoela*, a view which has already been more or less distinctly enunciated by several writers. Morphologically we may regard the radial chambers as diverticula from the primitive enteron. If we compare in *Alcyonaria* the histological structure of the walls of these chambers with that of the entodermic filaments, we find that the difference is exactly comparable with the difference between the mesodermic diverticula of *Sagitta* or *Amphioxus* and the walls of the enteron. The cells of the radial chambers, like those of the mesodermic diverticula, give rise to the muscular system, and according to the same type of histological differentiation; whereas the cells of the filaments, like those of the enteron, become specialised for the performance of the digestive functions. If the radial chambers became closed by the union of the mesenterial filaments, no-one would hesitate, either upon embryological, histological or physiological grounds,

to consider the radial chambers as a true coelom and their walls as a true mesoderm homologous with that, for instance, of *Amphioxus* or *Phoronis*.

We can carry this suggestion a step farther. With the exception of the anomalous *Haimeida* (which are very imperfectly known) all *Alcyonaria* show a pronounced bilateral symmetry. The cross-section of the body is more or less oval, the longer axis corresponding with the so-called dorso-ventral plane, and the mouth is greatly elongated in the same plane. With respect to this plane all of the organs are arranged in a bilateral symmetry, which is expressed not only in the adult structure but also in the embryology, as I have shown in the case of *Renilla*. We can therefore distinguish two terminal unpaired radial chambers and a series of paired lateral chambers. This suggests a direct comparison between the lateral radial chambers and the somites of segmented animals. Such a comparison may appear at first sight highly improbable. But if we compare the ideal section of a primitive eight-rayed polyp shown in fig. 16 with the embryo of *Peripatus*, as figured in BALFOUR's recent remarkable paper[1], or with HATSCHEK's figure of the embryo *Amphioxus*[2], the comparison loses some of its apparent absurdity. The similarity between the *Peripatus* embryo and the polyp is striking. Each has three lateral chambers (somites of *Peripatus*) derived in both cases, so far as the evidence shows, as outgrowths from the archenteron. Each has a slit-like primitive mouth, divided into a well-marked anterior and posterior division[3]. In *Peripatus* this primitive mouth closes in the middle, the anterior part becoming the embryonic mouth, the posterior part the embryonic anus. In *Alcyonaria* it does not close, but the two portions persist and perform different functions during a part or the whole of the life of the organism. It is well known that in many *Alcyonaria* there is a strongly marked ciliated groove, or rather a partly closed tube, on the »ventral« side of the oesophagus[4]. This division of the oesophagus performs the function of drawing water into the stomach, while the »dorsal« division is concerned with the ingestion of food. If these two

[1] Quart Journ. Micr. Sci., April 1883. Plate XX. fig. 35.

[2] Arb. d. Zool. Inst. Wien, Bd. IV, Heft I, Taf. IV, Fig. 47.

[3] In the diagram the mouth has very nearly the actual form it possesses in *Alcyonium* and many other *Alcyonaria*.

[4] See, for a brief notice of this structure a recent paper by HICKSON in the Proc. Roy. Soc. No. 226, 1880.

divisions should become morphologically as well as physiologically dis-
tinct by a longitudinal splitting of the oesophagus, accompanied by a
fusion of the mesenterial filaments, we should have an animal with
stomodaeum and proctodaeum, a closed mesenteron, and paired meso-
blastic somites. — Assuming for the moment the probability of such a
view, we may ask whether we can find any indications which division of
the oesophagus is to be regarded as the anterior one — that is as the
stomodaeum. In the *Alcyonaria* no such indications exist, on account of
the great abbreviation in the development, but in the *Cerianthidae* we
may possibly find the key to the problem. In this group a ciliated groove
exists, as in *Alcyonaria*, and according to the HERTWIGS is situated
upon the same side of the oesophagus, that is, the ventral.   The
principal septa decrease regularly in size from the ventral to the dorsal
side, and the HERTWIGS conclude that this represents the order of their
development in the embryo. In other words, the dorsal chambers are
the youngest, like the posterior somites of Annelides or Arthropods.
Hence, according to the view here suggested, the ventral division of
the oesophagus would represent the stomodaeum, and the dorsal division
the proctodaeum. — This view, if it should be shown to be well-founded,
would involve a completely new conception of the structure of a polyp.
The so-called oesophagus would represent the united stomodaeum and
proctodaeum of higher animals, and the so-called anal pore of *Cerianthus*
would not be in any way morphologically comparable with an anus. The
so-called dorsal and ventral surfaces would be respectively the poste-
rior and anterior extremities, the oral face would be ventral, and the
base or aboral extremity dorsal. The radial chambers and posterior
part of the stomach would represent the coelom, and the space between
the mesenterial filaments would correspond with the cavity of the me-
senteron.

It is perhaps hardly necessary to add that this comparison was
first suggested to me by BALFOUR's remarkable observations upon the
development of *Peripatus* (edited by MOSELEY and SEDGWICK) and that
it accords fully with his conception of the transition from radiate to bila-
teral animals. The comparison of the radial chambers of polyps with
the somites of *Peripatus* has, so far as I know, never been published.
It was however suggested by Mr. ADAM SEDGWICK in an oral communi-
cation to the Royal Society, in Dec. 1882, and at the same time he called
attention to the possible significance of the ventral groove of the oeso-
phagus (in *Peachia*). To him therefore belongs whatever credit may
attach to the origination of this comparison.

The state of our knowledge is too imperfect to admit of this suggestion being fully carried out at present, but I submit that the evidence is quite sufficient to warrant farther examination of the comparison.

Naples, Sept. 14, 1883.

Explanation of the Figures.

All of the figures, except the diagrams Nos. 14, 15 and 16, are drawn with the camera lucida. To avoid needless repetition, the general figures 5, 10 and 13 have each been constructed from two or three sections, and the histological detail in these figures is necessarily somewhat diagrammatic, although conveying a faithful picture of the points which are important for my purpose. The lettering, which is uniform throughout, is as follows.

a. a.   Openings of the finer canal-system into the main longitudinal canals.
c   Branches of the canal-system.
cx.   Calyx-teeth of the bud.
d.f.   Dorsal or ectodermic mesenterial filaments.
d.s.   Dorsal septa.
d.w.   Dorsal wall of stomodaeum.
ec.   Ectoderm.
e.f.   Entodermic mesenterial filaments.
en.   Entoderm.
m   Mouth.
mes.   mesoderm.
n   Fine branches of the canal-system.
oe   Oesophagus.
ov   Ova.
s   Septa.
sp.   Spicules.
v   Vacuoles in the entodermic filaments containing foreign bodies.
v. s.   Ventral septa.

Plate 1.

Fig. 1.   Young polyp of *Clavularia ochracea*, 14 days old, before the appearance of the stolon. Drawn from a preserved specimen. The dorsal filaments, *d.f.*, are less than half as long as the others. The line from *e.f.* extends to the dorso-lateral entodermic filament. × 65.

Fig. 2.   A longitudinal dorso-ventral section through the same individual, passing through the whole length of the dorsal filament, *d.f.*, and showing the connection of one of the ventral filaments, *e f.*, with the oesophagus. × 130.

Fig. 3.   View from the dorsal or inner side of a young bud of *Alcyonium palmatum* and a portion of the canal-system with which it is connected. The rudimentary dorsal filaments are shown at *d.f.*; *vl.f.* are the ventro-lateral, *dl.f.* the dorso-lateral, and *v.f.* the ventral filaments. The ventral and ventro-lateral filaments of one side have fused together. × 80.

Fig. 4.   Similar view of a much older, nearly half-grown bud of the same species.
          $\times$ 25.

Fig. 5.   Longitudinal section through a young sexual bud of *Kophobelemnon* from
          the lower part of the polyp–bearing region. The oesophagus is obliquely
          cut so that its communication with the exterior does not appear (for this
          see figs. 10. 13). The whole length of one of the dorsal filaments, *d.f.*,
          is shown, extending downwards into the canal-system. The latter com-
          municates at *a, a*, with the main longitudinal canals, and at *b* with the
          next younger polyp below. The upper part of the section is at the left
          hand. $\times$ 80.

Plate 2.

Fig. 6.   Cross-section through the dorsal filament of *Gorgonia verrucosa*. $\times$ 400.

Fig. 7.   Similar section through the dorsal filament of a young sexual polyp of
          Funiculina. $\times$ 400.

Fig. 8.   Similar section through the dorsal filament of *Paralcyonium*. $\times$ 400.

Fig. 9.   Similar section through the dorsal filament of a zooid of *Kophobelemnon*.
          $\times$ 400.

Fig. 10. Longitudinal section through a bud of *Alcyonium palmatum* slightly older
          than fig. 3. To the right — which is the side turned towards the end of
          the branch — the cavity of the bud overlies an older polyp, *P*, and at the
          left or lower end it communicates with the canal-system. $\times$ 80.

Fig. 11. More highly magnified view of the rudiment of the ventral filament shown
          at *e.f.* in fig. 10., showing its connection with the ventral wall of the
          oesophagus *v.w.*, at *in*. At *v* is a vacuole containing a foreign body.
          $\times$ 400.

Fig. 12. Cross-section of one of the entodermic filaments of *Paralcyonium*. At *d*
          is a diatom embedded in the filament. *nc.* nettle-capsules. $\times$ 400.

Fig. 13. Longitudinal section through three buds of *Funiculina*. In the youngest,
          A, the dorsal filaments, *d.f.*, are quite rudimentary and the entodermic
          filaments have not yet appeared. In B the dorsal filaments have attained
          a considerable length, and a slight accumulation of entoderm-cells at *e.f.*
          probably marks the beginning of one of the ventral filaments. In C
          the dorsal filaments are very long and the entodermic filaments, *e.f.*, are
          distinctly visible. At *v* are vacuoles containing food-particles. $\times$ 130.

Fig. 14. Diagram constructed from a figure by KÖLLIKER, of six polyps from the
          leaf of *Halisceptrum*, showing the dorsal filaments.

Fig. 15. Semi-diagrammatic figure of a portion of a branch of *Alcyonium palma-
          tum*; *p.* young buds, *P.* older polyps. The long axis of the figures cor-
          responds with that of the branch. The dorsal septa and filaments are
          diagrammatically represented at *d.f.* $\times$ 3.

Fig. 16. Diagram of a cross-section of a simple eight-rayed polyp to show its
          relations whith an animal possessing stomodaeum, proctodaeum and a
          segmented coelom. In the centre is the elongated oesophagus with the
          form it possesses in *Alcyonium*, showing the dorsal (*d.d.*) and ventral
          (*v.d.*) divisions. *d.p.* »glandular« portion of filament, *e.p.*, non–glandu-
          lar portion (cf. Fig. 12). The dotted lines represent the supposed union of
          the filaments and the splitting of the oesophagus into two distinct tubes.